Evidence of climate-induced range contractions for bull trout (Salvelinus confluentus) to cooler, higher-elevation sites in a Rocky Mountain watershed, U.S.A.

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Running title: Climate-induced range contraction of bull trout

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Abstract

Many freshwater fish species are considered to be particularly vulnerable to stream temperature warming associated with climate change because they are ectothermic, yet there are surprisingly few studies documenting changes in distributions. Streams and rivers in the U.S. Rocky Mountains have been warming for several decades. At the same time these systems have been experiencing an increase in the severity and frequency of wildfires, which often results in habitat changes including increased water temperatures. We resampled 74 sites across a Rocky Mountain watershed 17 to 20 years after initial samples to determine whether there were trends in bull trout occurrence associated with temperature, wildfire, or other habitat variables. We found that site extirpation probabilities (0.36) were significantly higher than colonization probabilities (0.13), which indicated a reduction in the number of occupied sites. Extirpation probabilities were greater at low elevations with warm temperatures. Other covariates, such as the presence of wildfire and various stream habitat descriptors, were not associated with extirpations. Even though this is a single river basin, higher extirpation probabilities at low elevation for bull trout provide initial evidence validating the predictions made by bioclimatic models that bull trout will retreat to high, cool thermal refuges as water temperatures increase. The geographic breadth of these declines across the region is unknown but the approach of revisiting historical sites using an occupancy framework provides a useful template for additional assessments.

Introduction

Global climate change is altering the distribution and abundance of many thermally sensitive taxa (Root *et al.,* 2003; Thomas *et al.,* 2004; Lenior *et al.,* 2008). Range shifts have been well demonstrated for some groups e.g., butterflies and plants (Parmesan & Yohe, 2003; Wilson *et al.,* 2005; Parmesan, 2006; Lenoir *et al.,* 2008). Aquatic organisms in freshwater ecosystems are expected to be particularly sensitive to climate shifts because most are ecothermic and have a relatively narrow thermal range for growth and survival (e.g., Elliott & Hurley, 2001; McMahon *et al.,* 2007; Elliott & Elliott, 2010). Although freshwater systems host a disproportionately large amount of the Earth's biodiversity, including many fish species of economic and cultural value, (Dudgeon *et al.,* 2006), observations of climate-related shifts in freshwater species distributions are confined to a few species in central and southern Europe (Hari *et al.,* 2006; Winfield *et al.,* 2010; Almodovar *et al.,* 2011; Comte & Grenouillet, 2013). That such observations are rare is surprising given that climate change is a global phenomenon.

One region where shifts in aquatic species distributions may be underway is the northern Rocky Mountains, U.S.A. where population boundaries of native salmonid species (e.g., bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarkii lewisi*; Dunham *et al.,* 2003; Sloat *et al.,* 2005) and competitive outcomes between native and nonnative species (McMahon *et al.,* 2007) are mediated by temperature (Isaak *et al.,* 2012a). Recent climate trends in this region include reduced annual snowpack, earlier annual peak snowmelt, and at lower elevations a shift in winter precipitation from snow to rain (Mote *et al.,* 2005, 2006; Knowles *et al.,* 2006). These factors contribute to lower summer base flows (Leppi *et al.,* 2012) and warmer summer water temperatures (Isaak *et al.,* 2012b). Increases in summer water temperatures of up to 0.3 °C/decade have been documented for Rocky Mountain river basins (Isaak *et al.,* 2012b).

Bioclimatic models assume that distributions of many fish species will track suitable thermal habitats by shifting to higher elevations as warming proceeds, which could result in range contractions and even population extirpations for some cold-water species (Keleher & Rahel, 1996; Rieman *et al.,* 2007; Williams *et al.,* 2009; Wenger *et al.,* 2011a,b). The most common prediction from these models is that cold-water species occurrence will decline in warm, low-elevation sites (Keleher & Rahel 1996; Rieman *et al.,* 2007; Williams *et al.,* 2009).

Most bioclimatic model predictions ignore the effects of other natural disturbances that are projected to change in the future, such as wildfire and flood regimes (but see Wenger *et al.,* 2011a,b for including changes to flood regimes). The western U.S. has experienced larger and more severe wildfires in recent years, a phenomenon attributed to climate change (McKenzie *et al.,* 2004; Running, 2006, Westerling *et al.,* 2006). Wildfires can increase stream temperatures by reducing riparian vegetation, important for shading streams from solar exposure (Dwire & Kauffman, 2003; Shakesby & Doerr, 2006; Pettit & Naiman, 2007). Following large stand-replacing fires, summer stream temperature often increase from 0.4 to 3.7 °C and these changes may persist for decades (Dunham *et al.,* 2007; Mahlum *et al.,* 2011). Consequently, one might expect the decline or disappearance of thermally sensitive fauna in those areas. But the short- and long-term effects of wildfire on native fish species are equivocal and likely depend on the life history, population size, and distribution of the affected species, as well as the characteristics of the fire (Burton, 2005; Kennedy *et al.,* 2009; Neville *et al.,* 2009; Sestrich *et al.,* 2011). Regardless, understanding whether fire-related disturbances and regional environmental changes combine to affect sensitive species is necessary to forecast species responses.

Perhaps the most thermally restricted fish species in the northern Rocky Mountains is the bull trout, which requires colder temperatures for juvenile rearing than any other fish in this region (Rieman *et al.,* 1997; Selong *et al.,* 2001; Isaak *et al.,* 2010). As a result, juvenile bull trout generally occupy cooler streams across the upper elevations of river networks, with the upstream extent of individual populations limited by steep slopes and small channels (Rieman & McIntyre, 1995; Wenger *et al.,* 2011a). Regional temperature increases associated with climate change have led to dire predictions about the persistence of this species in the U.S. (Rieman *et al.,* 1997; Wenger *et al.,* 2013), but there is little empirical evidence of climate-related shifts. Such information is of interest because of the federal listing of bull trout under the Endangered Species Act and the occurrence of this species across broad areas where it affects land management decisions.

In this study, our goal was to repeat a late 20th-century inventory of bull trout in a portion of western Montana to assess changes in the distribution of this species. Our objective was to compare reach-scale extirpation and colonization rates to determine whether they were different and if so, examine whether they were associated with site-level characteristics including wildfire occurrence and severity, habitat attributes including gradient, width, large woody debris, and temperature, and biotic variables such as brook trout presence and distance to where bull trout were common in main-stem river segments (Rich *et al.,* 2003). If the range of bull trout contracted, we expected site-level extirpation rates to be greater than colonization rates, particularly at the warmest sites. In addition, we examined how well elevation, often a surrogate for temperature for predicted changes in distributions attributed to climate change, was correlated with extirpation and colonization rates.

Materials and methods

Study area and species

The East Fork Bitterroot River basin is a 1,055-km^2 watershed in west-central Montana, U.S.A. (Figure 1). The basin is mainly a forested landscape with lower elevations dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii)* and higher elevations by lodgepole pine (*P. contorta* var. *latifolia)*, subalpine fir *(Abies lasiocarpa),* and Engelmann spruce (*Picea engelmannii).* The watershed is a temperate, snowmelt-dominated system with a range of elevations from 1,220 to 2,887 m. Arno *et al.,* (2000) described the historical fire regime for this area as mixed-severity with mean fire frequencies of 11 to 30 years. In 2000, wildfires burned 52.0% (29.2% at moderate to high severity) of the basin and 3.8% (2.5% at moderate to high severity) in 2007. Maximum summer stream temperatures in reaches where moderate- to high-severity fires burned in riparian stands remain elevated 1.4 to 2.2 °C above those from reaches adjacent to unburned stands (Mahlum *et al.,* 2011). Over a comparable interval (1999–2007) summer stream temperatures at unburned sites also increased 0.30 °C (July) and 0.17 °C (August; Mahlum *et al.,* 2011), which is similar to the July/August 0.24 °C/decade increase described for the Greater Yellowstone area (Isaak *et al.,* 2012a) and 0.22 °C/decade increase across the U.S. Northwest (Isaak *et al.,* 2012b). Average daily maximum summer water temperature increases are apparent in the main-stem East Fork Bitterroot River since 1995 (Figure 1). Similarly, summer air temperatures at the weather station nearest our study area (Sula, MT) have also increased over the last two decades.

The East Fork Bitterroot River is a core conservation area for bull trout (MBTSG, 1995; MBTRT, 2000). This watershed consists primarily of public land administered by the U.S. Forest Service (USFS) and has no known barriers to fish movement within our study area (MBTSG, 1995; MBTRT, 2000). Bull trout in this basin exhibit partial migration, with resident and migratory individuals in most spawning tributaries. Resident individuals spend their entire lives within their natal stream or tributary, moving only short distances (e.g., <2 km), whereas migratory individuals spawn in headwater tributaries but migrate to the river to forage (Fraley & Shepard, 1989; Nelson *et al.,* 2002; Al-Chokhachy & Budy, 2008). Other native fish in the basin include westslope cutthroat trout, slimy sculpin (*Cottus cognatus*), longnose dace (*Rhinichthys cataractae*), mountain whitefish (*Prosopium williamsoni*), and longnose suckers (*Catostomus catostomus*). Brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), and rainbow trout (*O. mykiss*) are non-native species present in the basin.

A number of factors influence bull trout habitat occupancy in its U.S. range. As noted earlier, bull trout require cold water (Rieman *et al.,* 1997; Selong *et al.,* 2001; Dunham *et al.,* 2003; Isaak *et al.,* 2010) and site occupancy of juvenile or resident bull trout is strongly correlated with maximum temperatures (Dunham *et al.,* 2003; Isaak *et al.,* 2010). However large individuals with migratory life histories are not restricted to cold thermal environments and can move through much warmer waters (e.g., 21°C 7-day average daily maximum temperature; Howell *et al.* 2010) before reaching spawning areas. Bull trout are also associated with relatively large patches of connected, complex habitat (Rieman & McIntyre, 1993; Watson & Hillman, 1997; MBTRT, 2000). In the Bitterroot River basin, the probability of bull trout presence in stream reaches was positively correlated with large woody debris, stream width, and relative abundance of main-stem bull trout at a tributary mouth, and negatively correlated with stream gradient and the presence of brook trout (Rich *et al.,* 2003).

Data collection

Rich *et al.,* (2003) sampled 1st- through 4th-order streams between 1992 and 1995 to determine bull trout occupancy patterns in the Bitterroot River basin, MT. In this sampling, three 500-m study sites were equally spaced over the estimated length of suitable habitat in each tributary. Between 2009 and 2011, we revisited 74 sites on streams sampled by Rich *et al.,* (2003) within the connected portions of the East Fork Bitterroot River basin to examine whether bull trout occupancy had changed. We relocated the sites and replicated the sampling methods of the earlier study. Fish were collected with a single-pass survey using a backpack electrofishing unit during the summer low-flow period. Care was taken to electroshock slowly and inclusively through all areas of cover. Our resampling was confined to 1st- through 3rd-order streams that were small enough to effectively sample with a backpack electrofishing unit. As in the previous study, we divided each site into five sequential 100-m sections for sampling. All fish were identified to species, counted, and measured (total length). Similar to Rich *et al.,* (2003), we strove to avoid basing bull trout presence on an itinerant adult. Therefore, presence in a section was defined by the capture of ≥ 2 bull trout, at least one of which was less than 250 mm.

We used field measures and GIS spatial data layers to assess covariates potentially related to bull trout occupancy. We counted large woody debris in the first 100-m section of every 500-m site. We estimated bankfull width (m) for the section by measuring it at three representative locations. Elevation (m) was noted in the field from the GPS unit (Garmin 60CSx) and validated from the 30-m cell size U.S. Geological Survey (USGS) National Elevation Dataset (USGS, 2006). Gradient at each site was derived from this dataset using TauDEM software (Tarboton, 2008). We used estimates of bull trout abundance in the main-stem East Fork Bitterroot River (http://fwp.mt.gov/fishing/mFish/newSearch.html; accessed 8/2/13) to assess the proximity of sites to main-stem locations where adults were captured commonly. We categorized sites into three groups: (0) bull trout common in the main-stem East Fork Bitterroot River at the tributary mouth; (1) bull trout common in the main-stem within 2.5

km of the tributary mouth; and (2) bull trout common in the main-stem >2.5 km from the tributary mouth.

We obtained fire severity GIS layers from the Bitterroot National Forest (Hamilton, MT). Burn severity is used to describe the amount of fire-related change including overstory vegetation mortality, soil heating, and fuel consumption (Keane *et al.,* 2008; Keeley, 2009). As in Mahlum *et al.,* (2011), our sites within moderate- and high-severity riparian burns had the majority of the riparian area (and watershed) burned, thus fire severity and proportion of site burned were positively related. We grouped burn severity into two categories and at each site we indicated whether the riparian area experienced no-to-low severity burns or medium-to-high severity burns.

Stream temperature model predictions

Because we did not have a single year with temperature data at every site and annual variation in temperature is large, we used a stream temperature model that allowed standardized representation of relative temperatures among sites. Holsinger *et al.,* (in review; Holsinger & Keane, 2011) developed a stream temperature regression equation and linked it to a landscape simulation model which allowed us to predict relative stream temperatures at fish sampling locations. The regression equation was developed using data from 116 temperature logger sites collected across a range of burn severities and in unburned sites for the years 2000 to 2009, mainly during the summer period July 15–September 30 (USFS, University of Montana, and Montana Fish, Wildlife and Parks, unpublished data). Predictors for the stream temperature regression equation were derived from a spatially explicit landscape model, FireBGCv2, and from topographic features (Holsinger *et al.,* in review; Keane *et al.,* 2011). FireBGCv2 predictors were air temperature, stream flow, and radiation at the stream surface and the geomorphic predictors included elevation, channel slope, and watershed contributing area. We calibrated the FireBGCv2 model to the East Fork watershed using spatial inputs based on 2004 satellite imagery such that model output represented conditions (loss of canopy cover and increased solar radiation) after the 2000 fires. The daily mean stream temperature (Y, in °C) equation was:

$$Y = 11.0 + 0.501(\text{daily average air temperature, °C}) - 0.236(\text{streamflow, m}^3\ \text{sec}^{-1}) + 0.0191(\text{stream flow} \times \text{daily average air temperature}) + 0.00160(\text{solar radiation, watts m}^{-2}) - 0.00536(\text{elevation, m}) - 2.98(\text{channel slope, drop over length}) + 0.00000000166(\text{contributing area, m}^2)$$

The regression equation accounted for a large portion of the daily stream temperatures variability (daily mean R^2 = 0.78, RMSE = 1.54 °C), and validation comparisons with independent data (August 2010 through August 2011) indicated that predictions compared reasonably well to field observations (r_s = 0.83, RMSE = 3.42 °C).

Our goal for using modeled stream temperature in the analysis was to standardize temperatures so that it was possible to accurately portray relative temperature differences among sites that we revisited to explore changes in bull trout occupancy in warmer versus cooler areas. These model-derived temperature differences reflected both site differences associated with landscape position (air temperature, elevation, and contributing area) and solar radiation at a site after the 2000 wildfires. To differentiate sites that were consistently warmer across the landscape, we calculated residuals for each site by subtracting the average basin-wide predicted temperature from the predicted temperature of each site for each year (from 2000 to 2009). We then summed these temperature residuals across the time period 2000–2009 to ensure that sites that were consistently warmer had greater positive residuals and sites that were consistently cooler had larger negative residuals. We used these summed temperature residuals as a covariate in the analysis.

Data analyses

Incorporating probability of detection

Species are rarely detected perfectly. Therefore, naïve detect-nondetect data that are uncorrected for detection probability will typically underestimate occupancy and provide biased estimates of colonization and extirpation rates (MacKenzie *et al.,* 2003; Bailey *et al.,* 2004). Repeated assessments of sites (assuming occupancy remains static) can be conducted at the same location but partitioned by time, observer, or methods, or conducted at different locations within a site (MacKenzie *et al.,* 2006). To account for variation in probability of detection we used program PRESENCE 4.1 (Hines, 2006) to estimate detection probability, occupancy, and extirpation or colonization rates.

The probability of occupancy parameter is the proportion of sites that are occupied corrected for the probability that the species has been missed. We constructed a survey history based on the five, 100-m sections for each site across the 1992–1995 and 2009–2011 surveys. These separate survey intervals were regarded as seasons. Estimates for probability of detection were modeled as a function of the standardized covariates (season, large woody debris, fire, width, and gradient) that might influence detection probability. Because large woody debris and the occurrence of medium- to high-severity fire at the site change over time, we used these as survey-specific covariates. Given that both survey events had imperfect detectability and different crews (but the same field protocol), we compared whether detection probability differed between the two seasons. In addition, we explored all possible combinations of covariates (season, survey-specific large woody debris and fire, site-specific width and gradient) in competing models to examine which covariates best described the probability of detection across sites and whether probability of detection differed between the earlier and more recent surveys (based on maximum likelihood estimators and Akaike Information Criterion (AIC); Burnham & Anderson, 2002).

What factors were associated with site extirpation or colonization rates of bull trout?

We used a multi-season model. The model uses initial occupancy estimates for the first sampling period and derives estimates for the extirpation and colonization rates that determine whether a species occurs at a site during the second sampling period. Therefore with the second sampling session, one can estimate extirpation and colonization rates (Donovan & Hines, 2007). To examine changes in occupancy in our data set, we first determined whether estimates of bull trout extirpation (ε) or colonization (γ) rates were significantly different from zero and from one another. For example, if these rates were not different from zero, there was not a substantial shift in the occurrence of bull trout across the landscape. If these rates are greater than zero but similar and not associated with our covariates then bull trout occupancy could be changing at random. Finally, we tested whether large woody debris, gradient, width, brook trout presence, proximity to where bull trout were common in the main-stem, occurrence of medium- or high-severity fire, or relative temperature co-varied with estimated bull trout extirpation or colonization rates. In addition, we examined how elevation co-varied with colonization and extirpation rates to evaluate whether elevation was a good surrogate predictor of changes in bull trout distribution. Models were fit using maximum likelihood estimators and ranked based on AIC scores (Burnham & Anderson, 2002). We considered all models within 2 AIC units of the top model, but disregarded uninformative parameters i.e., covariates for which the absolute value of β/SE < 1.4 which indicates approximate 85% confidence intervals overlapped zero (85% confidence intervals were used to be AIC compatible, see Arnold, 2010). We also performed stepwise variable removal, based on the minimum absolute value of β/SE, stopping when variable exclusion led to a decrease in AIC score for the model (Arnold, 2010).

Results

We detected bull trout at 20 of the 33 sites where they were previously observed (13 potential extirpations). Of the 41 sites without bull trout in the original survey, we detected bull trout at 5 sites. At these sites, brook trout occupancy slightly declined between the earlier (12 sites on 6 streams) and later (7 sites on 5 streams) surveys. In addition, thirty-one of the 74 sites had adjacent riparian burns during the period between surveys, 12 of which were from medium- to high-severity fires.

Incorporating probability of detection

There were no significant correlations among covariates used to explain probability of detection (large woody debris, width, gradient, occurrence of medium- to high-severity fire). Therefore, we compared all possible combination of covariates that may have influenced detection probability and tested whether there was a difference in detection between seasons. There were three top models (within 2 AIC units of each other) and none included fire (Table 1). Our naïve (no covariates) probability of detection estimate was 0.54 (SE, 0.03). Naïve detection probabilities did not differ between seasons (season 1: 0.54, SE 0.04; season 2: 0.54, SE 0.06) and this variable (season) did not increase the model AIC score. Therefore, the top model for estimating probability of detection included only large woody debris and width as covariates. Based on this model, site-specific probability of detection varied from 0.09 to 0.99 (Supplemental Table 1).

What factors were associated with site colonization or extirpation rates of bull trout?

After fitting the probability of detection function, we examined correlations among predictor variables (Supplemental Table 2) and evaluated all covariate combinations for their effects on colonization and extirpation probabilities except elevation. Elevation and temperature were negatively correlated (-0.59) and brook trout were present in warmer sites on the landscape (0.56). Elevation was only considered as a single predictor since our question related to how well it performed as a single surrogate for many of the mechanistic landscape patterns such as temperature. The overall (no site or survey covariates) extirpation rate (0.36, SE 0.07) was almost 3-fold greater than the colonization rate (0.13, SE 0.07).

Most covariates in models for estimating colonization or extirpation rates were uninformative because of small effect sizes or large standard errors. The three top models with informative covariates for extirpation probabilities included either no covariate or the single covariates of elevation or temperature (bolded in Table 2). We model averaged the top three models with informative parameters. Estimated extirpation rates increased approximately 3-fold from cooler to warmer sites (Figure 2) and high- to low-elevation sites (Figure 3). No informative covariates were retained in the top model for estimating colonization.

Discussion

Bioclimatic models accounting for climate change predict an array of phenological changes and range shifts in freshwater aquatic species (Ficke *et al.*, 2007; Beer & Anderson, 2013). Alteration in the timing of life history events has been relatively widely observed (Wedekind & Küng, 2010; Crozier *et al.*, 2011; Warren *et al.*, 2012). In contrast, confirmation of predictions that stenothermic cold-water fishes should be undergoing distributional shifts to cooler, high-elevation refuges has been elusive (but see Hari *et al.,* 2006; Comte & Grenouillet, 2013), particularly in North America (Isaak & Rieman, 2013). By revisiting historically sampled sites within a river network that encompasses a broad temperature and elevation gradient, we demonstrated that extirpation rates of bull trout were highest at warmer, low-elevation sites over the last two decades. This coincided with increases in summer stream temperatures in the East Fork Bitterroot River basin by as much as 0.30 °C (July temperatures; Mahlum *et al.,* 2011). Moreover, neither colonization nor extirpation rates were related to variables reflecting habitat, biotic interactions, or recent disturbance. Collectively, we believe this study substantiates predictions of this pattern in other studies (Rieman *et al.*, 2007; Isaak *et al.*, 2012a; Ruesch *et al.*, 2012).

Only those covariates most closely related to the decreased thermal suitability of bull trout habitat—water temperature and elevation—appeared in the top models for estimating extirpation rates. This may seem surprising, given that occupancy models for bull trout have included an array of habitat and biotic variables (Rich *et al.*, 2003; Wenger *et al.*, 2011a). A critical distinction is that we did not model where bull trout are currently found; rather, we examined what influenced changes in that distribution over the last two decades. Consequently, it might be expected that elevation (represented in a linear function across a broad range) would not explain the distribution of bull trout in the Bitterroot River basin (Rich *et al.*, 2003), but was our best predictor of locations from which bull trout would be extirpated. We attribute most of the explanatory power of elevation in our model to its relation to water temperature, but acknowledge that it can, in part, represent effects of other variables, such as the presence of nonnative species or the effects of fire. In this study, however, neither were informative contributors to models of changes in bull trout occupancy. At the sites we examined in the East Fork Bitterroot River, brook trout occupancy was low and declined over our study period. Our temperature modeling accounted for reduced canopy cover associated with the major wildfires in our study area to predict differences in summertime temperature across the landscape each year. So, if this resulted in these sites becoming the warmest sites in the basin each year then the fire and temperature predictors would be linked. The low elevation sites in the basin that burned were some of our warmest sites, but there was not a correlation (0.45) between relative temperature and fire due to the occurrence of wildfire across the entire watershed. In addition to temperature, the presence of medium to high severity fire would have reflected other influences on habitat, such as increased autochthonous productivity, macroinvertebrate community shifts, or channel alteration (Gresswell, 1999). That no studies have demonstrated persistent losses of bull trout populations (or other non-isolated populations of stream salmonids; Rieman & Clayton, 1997; Howell, 2006; Dunham *et al.*, 2007; Sestrich *et al.*, 2011, Rosenberger *et al.,* 2012) implies that concerns about the consequences of wildland fire for many stream salmonids may, in many cases, be overstated (Burton, 2005). Nevertheless, because stand-replacing fire in riparian zones leads to chronic increases in summer stream temperatures (Dunham *et al.*, 2007; Mahlum *et al.*, 2011) it has the potential to contribute to local, site-specific changes in occupancy by bull trout. Anticipated increases in fire extent or frequency attributable to climate change

(Westerling *et al.*, 2006) may lead to more profound shifts, or outright extirpations, of populations across the landscape, in particular where populations are isolated or landscapes are more prone to large, post-fire debris flows.

Connectivity has long been thought to influence the persistence of salmonid populations because these fishes can be highly mobile and frequently form metapopulations (Rieman & Dunham, 2000). In our analyses, rank distance to the main-stem river sections where bull trout are common did not markedly account for the probability of extirpation or colonization at tributary sites, despite that the previous model of bull trout occupancy in this basin (Rich *et al.*, 2003) included a similar variable. Applying our rule set for excluding uninformative variables, however, would also have excluded this variable from the earlier occupancy model. One explanation for the relative unimportance of connectivity in our study might be that the distances involved (a few tens of kilometers at most) do not represent meaningful levels of isolation for bull trout, migratory forms of which often traverse much longer distances (Bjornn & Mallet, 1964; Fraley & Shepard, 1989). Genetic evidence indicates that despite declines in the abundance of migratory bull trout in the East Fork Bitterroot River basin over the last few decades, dispersal by bull trout among tributaries and between tributaries and the main-stem East Fork Bitterroot River remains common (Nyce *et al.*, 2013). If climate change or anthropogenic habitat alteration lengthens the distance between suitable rearing habitats or between rearing and spawning habitats, the energetic and demographic costs of migration may cross a threshold that makes the influence of connectivity more evident (Starcevich *et al.*, 2012).

Although occupancy modeling is becoming fairly common, it is only beginning to be used to model changes in species presence across the landscape (e.g., Altwegg & Wheeler, 2008; Moritz *et al.,* 2008). Occupancy modeling can be constrained by differences in sampling design, non-detection issues (from differences in methods, time, date, weather, habitat), and false detection issues (primarily misidentification; Tingley & Beissinger, 2009). But for species that are easily identified, there are monitoring efforts and previous studies that we can take advantage of in order to resample either in a paired manner (resampling same sites) or unpaired manner (resampling different specific sites but across the entire environmental gradient within the same locality (Tingley & Beissinger, 2009).

Ideally, one would have within-season (over time within a closed season) resampling to explicitly evaluate detection probability to incorporate in an occupancy model, but if this is not possible then sampling similar habitat in the same locality (site), as was done in this study, can be used to estimate probability of detection (see MacKenzie *et al.,* 2006; Tingley & Beissinger, 2009) if certain assumptions are met, such as resampling with replacement or if the species is mobile (Kendall & White, 2009). Potential bias in substituting space for time, could result in a lower estimate of occupancy than “truth” if few localities (reaches) within a site are occupied. Thus, this could bias our estimates of extirpation rates, if bull trout occurred in more reaches per site in the Rich *et al.,* (2003) study and fewer reaches per site in our study. However this did not occur within our dataset; where bull trout were present at a site the average proportion of 100-m reaches occupied per 500-m site was similar between datasets (0.55 in season 1 versus 0.65 in season 2).

That range shifts among freshwater species have been difficult to detect may seem ironic, given that these taxa may be among the most sensitive to climate change. This could be partly attributable to a paucity of suitable data sets. Adequately georeferenced historical data sets are relatively rare, particularly those that include habitat characteristics that could influence detectability. Nevertheless, the enormity of current and historical fish monitoring efforts by state, tribal, and federal agencies throughout North America suggests that many such data sets exist. Although many are likely to lack historical stream temperature records, recent advances in modeling dendritic ecological networks (Peterson *et al.*, 2013) can facilitate more accurate hindcasting and prediction of stream temperatures for basins well represented by recent temperature records (Isaak *et al.*, 2010).

Other obstacles to detecting the effects of climate change on cold-water fishes reflect their habitat and biology. Although rising water temperature appears to be a consistent trend in many portions of the historical range of bull trout and other western North American salmonids (Isaak *et al.*, 2012a,b), uncertainty about the response of particular watersheds remains high (Arismendi *et al.*, 2013). Fish abundance is known to be exceptionally temporally variable and to sometimes require decades of sampling before statistically significant trends emerge (Maxwell & Jennings, 2005; Al-Chokhachy *et al.*, 2009). In addition, such trends may be superimposed on long-term variation in abundance dictated by climate cycles such as the Pacific Decadal Oscillation (Mantua *et al.*, 1997). Nevertheless, correlations between bull trout abundance and broad-scale climate cycles (or this species' abundance and that of other salmonids) are weak (High *et al.,* 2008; Copeland & Meyer, 2011). Analyses that rely on occupancy, rather than abundance, may also be less vulnerable to temporal fluctuations. Nonetheless, extending the current time series of observation of bull trout in the East Fork Bitterroot River basin, as well as adding similar observations from other basins, are essential to evaluating the generality and permanence of the patterns we have observed.

In summary, we found that in this core, connected conservation area for bull trout, patterns in local extirpation were consistent with the predicted effects of stream temperature warming, which has been previously demonstrated in this basin. We acknowledge that these findings reflect patterns from only one river basin. In other basins with different species assemblages and impacts, these patterns likely interact with exotic species (Rahel *et al.,* 2008), anthropogenic habitat loss, and population fragmentation (Rahel *et al.,* 1996). Nevertheless, their consistency with predictions from bioclimatic models highlights the need to examine basins throughout the range of bull trout (and other aquatic species) to improve our understanding of how cold-water species may be altering their distributions through time. To that end, revisiting historically sampled sites across a range of elevations within a stream network to examine changes in occupancy constitutes a powerful approach for exploring the effects of climate change (Isaak & Rieman, 2013).

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Table 1: Models within 2 Akaike Information Criterion (AIC) of the top model for estimating probability of detection of bull trout with probability of occupancy, colonization, and extirpation held constant. The selected model (bolded) is the only one without uninformative variables. Abbreviations: W, width; LWD, large woody debris; S, season; G, gradient.

Model[1]	AIC	Delta AIC	AIC wt	Model likelihood	no. Par.	-2Loglike
$p(W_{4.22},LWD_{4.47})$	**479.22**	**0.00**	**0.5467**	**1.0000**	**6**	**467.22**
$p(S_{0.55}\,W_{4.22},LWD_{4.47})$	480.88	1.66	0.2384	0.436	7	468.04
$p(W_{4.22},LWD_{4.47},G_{0.35})$	481.09	1.87	0.2146	0.393	7	467.09

[1] Variables subscripted with β/SE absolute values.

Table 2. Models within two AIC units of the top model for using changes in occupancy (ψ) to estimate colonization (γ) and extirpation (ε) rates of bull trout. The selected models (bolded) are those without uninformative variables. Abbreviations: E, elevation; ; T, temperature; LWD, large woody debris; W, stream width; G, gradient; B, brook trout presence at site; D, distance to where bull trout are common in the main-stem East Fork Bitterroot River; F, occurrence of moderate- to high-severity fire. Parameter estimates for the untransformed coefficients in the best supported models (in bold) include E: -0.73 (0.46 SE) and T: 0.63 (0.44 SE).

Model[1,2]	AIC	Delta AIC	AIC wt	Model likelihood	no. par.	-2LogLike
$\psi, \gamma,\varepsilon(E_{1.59})$	**478.38**	**0**	**0.10**	**1**	**7**	**464.38**
$\psi,\gamma,\varepsilon(B_{0.5})$	478.62	0.24	0.088	0.88	7	464.62
$\psi,\gamma,\varepsilon(T_{1.43})$	**478.94**	**0.56**	**0.075**	**0.76**	**7**	**464.94**
ψ,γ,ε	**479.22**	**0.84**	**0.065**	**0.66**	**6**	**467.22**
$\psi,\gamma,\varepsilon(B_{0.47}, D_{0.73})$	480.11	1.73	0.042	0.42	8	464.11
$\psi,\gamma,\varepsilon(B_{0.46}, T_{0.72})$	480.12	1.74	0.042	0.42	8	464.12
$\psi,\gamma,\varepsilon(B_{0.66}, F_{0.73})$	480.12	1.74	0.042	0.42	8	464.12
$\psi,\gamma,\varepsilon(D_{1.04})$	480.17	1.79	0.040	0.41	7	466.17
$\psi,\gamma,\varepsilon(B_{0.24},G_{0.62})$	480.24	1.86	0.039	0.40	8	464.24
$\psi,\gamma,\varepsilon(T_{1.43}, LWD_{0.68})$	480.45	2.0	0.035	0.36	8	464.45

[1] All models contained the probability of detection function p(W, LWD).

[2] Variables subscripted with β/SE absolute values.

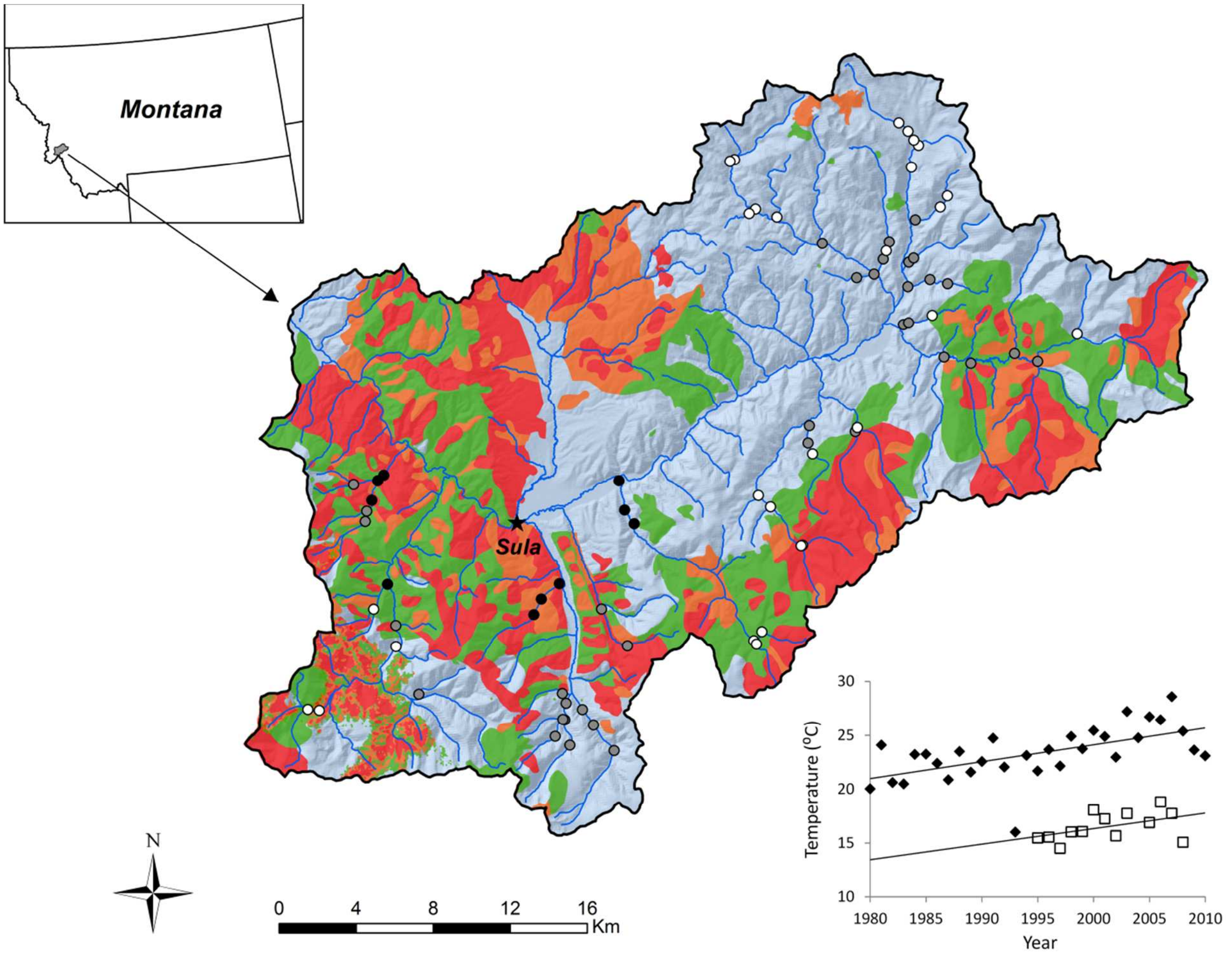
Figure captions

Figure 1. Sampling locations (500-m sites that were initially visited in 1992–1995 and resampled in 2009–2011) are shaded to indicate estimates of extirpation probability (white: 0.21-0.32, grey: 0.32 - 0.47, and black: 0.47 -0.62) in the East Fork Bitterroot River watershed. Burn severity for fires in the watershed is indicated by low severity in green, moderate severity in orange, and high severity in red. Grey is outside of the fire perimeters. Water and air temperature patterns within the East Fork Bitterroot River basin are inset. Black diamond symbols are average daily summertime (July and August) air temperature recorded over the study period at the closest weather station at Sula, MT ($y = 0.1567x - 289.27$, $R^2=0.34$, $p=0.0006$). Hollow squares are average daily maximum water temperatures over the summer season (July 15 to September 30) from the East Fork Bitterroot River main-stem 28.6 km upstream of the confluence with the West Fork Bitterroot River ($y = 0.1441x – 271.96$, $R^2=0.22$, $p=0.10$).

Figure 2. Model-averaged extirpation rates (filled diamonds) from the top three informative models (bolded in Table 2) with their upper and lower 95% confidence intervals (dashes) versus standardized relative temperature across sites in the East Fork Bitterroot River basin.

Figure 3. Model-averaged extirpation rates (filled diamonds) from the top three informative models (bolded in Table 2) with their upper and lower 95% confidence intervals (dashes) versus standardized elevation.

Figure 1:


Montana
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Temperature (°C)
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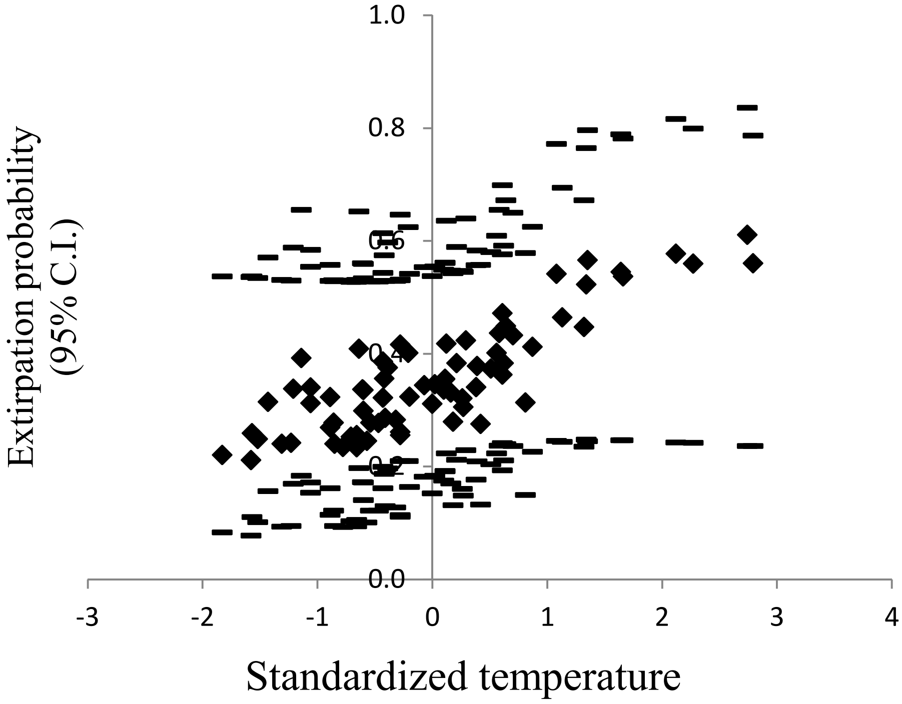
Year

Figure 2


1.0
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0.0
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1
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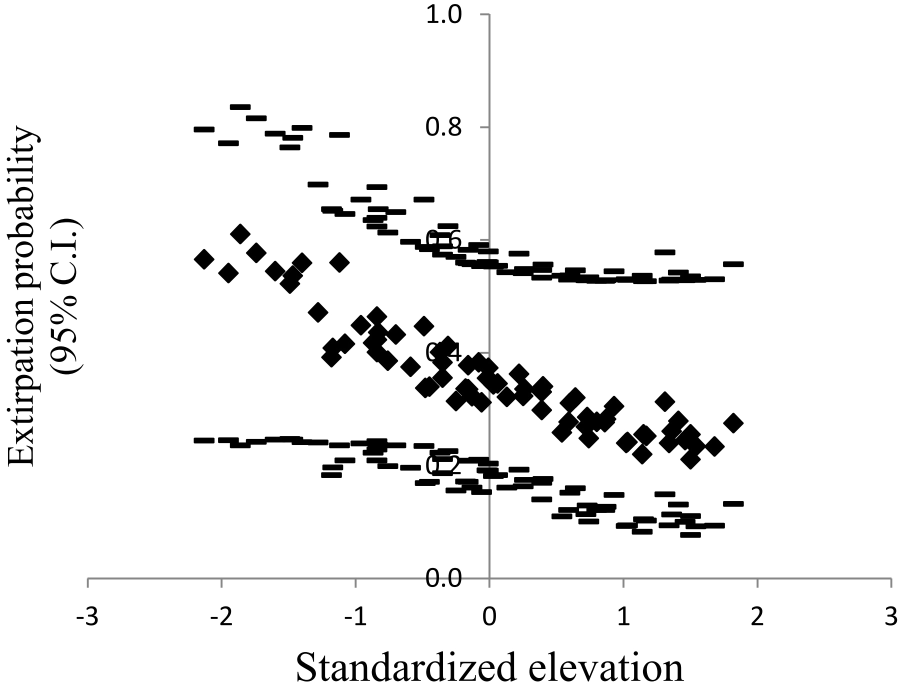
3
4
Extirpation probability
(95% C.I.)
Standardized temperature

Figure 3


1.0
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0.4
0.2
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-3
-2
-1
0
1
2
3
Extirpation probability (95% C.I.)
Standardized elevation

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Supplemental Table 1. Probability of detection without covariates was 0.54 (SE, 0.03). Detection probability associated with each site and each survey considering large woody debris during each survey and stream width at each site.

Survey_Site	Prob. Detection	Lower 95% CI	Upper 95% CI	Survey_Site	Prob. Detection	Lower 95% CI	Upper 95% CI
1_1	0.457	0.357	0.561	2_1	0.327	0.240	0.427
1_2	0.663	0.539	0.769	2_2	0.688	0.557	0.794
1_3	0.759	0.651	0.842	2_3	0.595	0.517	0.669
1_4	0.810	0.711	0.881	2_4	0.990	0.942	0.998
1_5	0.636	0.552	0.713	2_5	0.762	0.665	0.837
1_6	0.501	0.398	0.604	2_6	0.340	0.254	0.437
1_7	0.529	0.371	0.681	2_7	0.940	0.857	0.977
1_8	0.471	0.386	0.558	2_8	0.408	0.326	0.495
1_9	0.341	0.258	0.436	2_9	0.343	0.260	0.437
1_10	0.440	0.355	0.528	2_10	0.400	0.318	0.489
1_11	0.508	0.415	0.601	2_11	0.796	0.639	0.896
1_12	0.676	0.586	0.755	2_12	0.498	0.420	0.577
1_13	0.490	0.414	0.566	2_13	0.413	0.332	0.500
1_14	0.839	0.709	0.918	2_14	0.845	0.714	0.922
1_15	0.136	0.069	0.251	2_15	0.148	0.077	0.266
1_16	0.739	0.646	0.815	2_16	0.841	0.736	0.909
1_17	0.943	0.858	0.979	2_17	0.857	0.714	0.935
1_18	0.394	0.269	0.534	2_18	0.676	0.586	0.756
1_19	0.283	0.196	0.389	2_19	0.368	0.286	0.458
1_20	0.210	0.130	0.320	2_20	0.384	0.283	0.495
1_21	0.908	0.784	0.964	2_21	0.715	0.612	0.800
1_22	0.532	0.457	0.606	2_22	0.570	0.492	0.644
1_23	0.503	0.427	0.578	2_23	0.450	0.371	0.532
1_24	0.497	0.409	0.585	2_24	0.575	0.472	0.672
1_25	0.198	0.118	0.313	2_25	0.212	0.129	0.329
1_26	0.921	0.821	0.967	2_26	0.888	0.784	0.945
1_27	0.412	0.278	0.561	2_27	0.580	0.471	0.681
1_28	0.364	0.222	0.534	2_28	0.609	0.499	0.708
1_29	0.806	0.602	0.919	2_29	0.885	0.740	0.954
1_30	0.435	0.346	0.529	2_30	0.503	0.404	0.602
1_31	0.639	0.556	0.714	2_31	0.647	0.564	0.722
1_32	0.370	0.289	0.460	2_32	0.491	0.409	0.572
1_33	0.556	0.459	0.648	2_33	0.393	0.312	0.481
1_34	0.581	0.481	0.675	2_34	0.370	0.288	0.460
1_35	0.134	0.069	0.245	2_35	0.244	0.159	0.355

1_36	0.280	0.195	0.384	2_36	0.425	0.328	0.528
1_37	0.302	0.207	0.417	2_37	0.256	0.169	0.369
1_38	0.564	0.473	0.651	2_38	0.544	0.450	0.634
1_39	0.612	0.532	0.686	2_39	0.556	0.479	0.630
1_40	0.486	0.406	0.566	2_40	0.424	0.336	0.517
1_41	0.751	0.656	0.826	2_41	0.577	0.476	0.672
1_42	0.096	0.043	0.199	2_42	0.158	0.086	0.272
1_43	0.172	0.099	0.283	2_43	0.268	0.181	0.377
1_44	0.189	0.112	0.300	2_44	0.235	0.152	0.347
1_45	0.094	0.042	0.197	2_45	0.141	0.074	0.253
1_46	0.542	0.462	0.620	2_46	0.442	0.349	0.539
1_47	0.550	0.472	0.627	2_47	0.490	0.406	0.575
1_48	0.524	0.409	0.637	2_48	0.304	0.218	0.406
1_49	0.359	0.270	0.458	2_49	0.190	0.113	0.302
1_50	0.278	0.172	0.417	2_50	0.170	0.094	0.289
1_51	0.597	0.494	0.693	2_51	0.446	0.318	0.581
1_52	0.255	0.163	0.374	2_52	0.301	0.200	0.425
1_53	0.133	0.067	0.246	2_53	0.180	0.100	0.303
1_54	0.298	0.209	0.406	2_54	0.260	0.175	0.369
1_55	0.742	0.649	0.818	2_55	0.504	0.397	0.611
1_56	0.521	0.442	0.599	2_56	0.457	0.370	0.547
1_57	0.306	0.181	0.468	2_57	0.133	0.066	0.250
1_58	0.137	0.070	0.251	2_58	0.125	0.062	0.236
1_59	0.190	0.110	0.308	2_59	0.179	0.101	0.295
1_60	0.263	0.167	0.388	2_60	0.254	0.160	0.378
1_61	0.164	0.088	0.285	2_61	0.144	0.074	0.260
1_62	0.122	0.059	0.238	2_62	0.150	0.077	0.274
1_63	0.237	0.154	0.345	2_63	0.218	0.138	0.327
1_64	0.154	0.084	0.265	2_64	0.172	0.099	0.284
1_65	0.158	0.087	0.269	2_65	0.245	0.158	0.360
1_66	0.582	0.496	0.664	2_66	0.383	0.301	0.473
1_67	0.099	0.045	0.203	2_67	0.168	0.094	0.281
1_68	0.606	0.439	0.752	2_68	0.302	0.207	0.417
1_69	0.312	0.220	0.421	2_69	0.373	0.273	0.486
1_70	0.173	0.099	0.284	2_70	0.201	0.122	0.312
1_71	0.438	0.320	0.563	2_71	0.251	0.165	0.362
1_72	0.440	0.333	0.553	2_72	0.247	0.164	0.355
1_73	0.773	0.651	0.861	2_73	0.776	0.656	0.864
1_74	0.805	0.669	0.895	2_74	0.740	0.579	0.854

Supplemental Table 2. Pearson correlation coefficients for standardized variables in analyses including elevation (E), large wood debris (LWD), bank-full width (W), gradient at site (G), relative temperature (T), the presence of medium to high severity burns at the site (F), the presence of brook trout (B), and the distance from the tributary confluence to where bull trout are common in the main-stem (D). Elevation and temperature were negatively correlated (-0.59) and brook trout were present in warmer sites on the landscape (0.56).

	E	LWD	W	G	T	F	B	D
E	1.00							
LWD	0.14	1.00						
W	-0.03	0.34	1.00					
G	0.13	0.08	-0.12	1.00				
T	**-0.59**	-0.02	0.16	-0.19	1.00			
F	-0.25	0.13	0.03	0.05	0.45	1.00		
B	-0.45	-0.10	0.27	-0.17	**0.56**	0.11	1.00	
D	-0.46	-0.24	0.06	0.16	0.31	0.17	0.16	1.00

9/8/13

Global Change Biology Editorial Office,

Thank you for considering this manuscript. We have worked to substantially revise this manuscript based on the three generally positive reviews including making the specific suggested editorial changes, removing season and other uninformative parameters from the analysis (with a better treatment of them in the text as suggested by review 2) and adding distance to a river section where bull trout are common (as suggested by reviewer 3). Below you will see a point by point response of how we have considered the specific comments to be addressed (our responses are in red). We attempted to deal with every concern while still keeping the paper concise.

Sincerely,
Lisa Eby, corresponding author

Reviewer: 1

1. First paragraph in introduction. To provide additional context for the readers of GCB, consider a sentence or two describing levels of aquatic biodiversity relative to other taxa. The general point being that freshwaters host a disproportionately large amount of the Earth's biodiversity, yet we know relatively little about these systems. There's also some evidence of freshwater systems being degraded more rapidly and extensively than terrestrial systems.

We have revised the first paragraph to highlight the importance of freshwater ecosystems and their disproportionate high amount of biodiversity.

2. Line 99, start new paragraph at "In this study…" Also consider adding a separate objective before the one currently listed. That first objective would be simply determining whether rates of site extirpation/colonization were equal or significantly skewed across this landscape. The second objective then could be the current one, which is understanding the factors that contribute to site extirpations/colonizations.

We have revised to include the first objective examine whether they are different, and if so, whether they are associated with particular habitat and biotic characteristics.

3. Also near this section (line 101) specify that extirpations/colonizations are at a site or reach scale so readers understand the geographic context.

We have revised as suggested, including the modifier reach-scale.

4. Line 284. It would be useful to know how many of the 77 sites had brook trout during survey 1 and survey 2. This would give a more precise sense of whether their populations were expanding/stable/shrinking.

We have added this information to the text to highlight this point both in the results and in the discussion. Generally the occurrence of brook trout was relatively stable, if anything brook trout have become less abundant as a result of the 2000 fires.

5. Figure 1. The study basin and survey site map could be more informative by plotting the 77 sites using three types of symbols. 1 symbol designating sites where no change in occupancy status occurred between surveys; 1 symbol designating sites where an extirpation occurred; and 1 symbol where a colonization occurred.

We have revised Figure 1 based on this and additional reviewer comments. In this figure, the sampling locations are shaded depending on the extirpation probability (accounting for probability of detection). We have also added water temperature to the inset as suggested by a future reviewer.

6. Line 338 in discussion. Replace "longitudinal gradient" with "river network"
We have revised as suggested.

7. Lines 357/358. Last sentence of this paragraph seems like it belongs better with next paragraph.
We have revised as suggested.

8. Discussion pertaining to fire effects on bull trout distributions (page 19). An important point to consider may be that wildfires are one of the indirect mechanisms by which climate change will alter streams and forests over time. Rather than the effects of wildfires being transient as has historically been the case, it could be that forests in some of the burned areas will not recover to their pre-fire conditions and instead undergo conversion to more xeric types of vegetation. If that were to happen, wildfire could still have important long term effects on bull trout distributions and may act synergistically with other aspects of climate change to reduce the amount of coldwater habitats available to this species.
We have revised as suggested.

9. One significant contribution of this study is the rigor of the study design and occupancy analysis. As the authors describe, it could inform similar efforts in other portions of the species range and because of that, it would be good to know more details regarding the dataset. If it were possible, it would be useful to have a supplementary materials section that contained information on the site occupancy status at the 5 plots at each of the 77 sites, the numbers of fish caught at each site, and some of the covariate values. Another useful supplementary table would be one that compared naïve estimates of extirpation/colonization rates to those derived based on incorporation of detection efficiencies.

We are willing to put the data frame for the analyses (100m reach occupancy for each 500 site) and covariates in a supplemental materials file if our paper is accepted as suggested. We have added a supplementary table that includes the site-specific detection probabilities compared with the general probability of detection (no covariates).

Excellent study. Dan Isaak

Reviewer: 2

Comments to the Author
This is a good study and an important contribution, at least in the fish world. I have some quibbles with the statistical methods and would like to see some improvements to the discussion. See detailed comments below. Introduction: This is very well written and organized.

95. A better ref for this than Wenger et al. 2011 is a new paper by Wenger et al. in GCB. http://onlinelibrary.wiley.com/doi/10.1111/gcb.12294/abstract. I'm not necessarily suggesting that it be cited, just pointing it out.
We have revised as suggested and included Wegner et al. 2013.

141. Is it possible to cite the MFISH database?

If citing a Montana Fish Wildlife and Parks online database is okay with the editors, then this is fine with the authors and we have revised as suggested.

158. Why is Rieman and McIntyre cited here (also note misspelling of McIntyre)… is it for the method used by Rich et al? I would just cite Rich et al.
This was to highlight that the methods used by Rich et al. derived from Rieman and McIntyre as this reviewer intuited. Even so, we have revised as suggested and removed Rieman and McIntyre.

189. This is up to the editors, but I doubt it's going to fly to repeatedly cite an article in prep. Provide sufficient detail on the temperature model predictions here, or if necessary put additional detail into supplementary materials.
The Fire BGCv2 model has been published as we report (Keane et al. 2011). The additions to that model are the stream temperature predictions. There is a short report detailing the approach and the MS is currently submitted to Climatic Change. Even so, we have detailed the key components, including the number of loggers and time period the statistical model was fit to, the equation (predictor variables and betas) the variance described by the equation, as well as the validation procedure and fit. Certainly, we are not necessarily against adding specific requests to supplemental material, but we wanted to keep the manuscript text concise and focused. We feel that the information provided associated with what is already published is sufficient.

197-198. A simple rewording would make this less awkward. "We estimated stream temperature using a spatially-explicit landscape model, FireBGCv2, that was calibrated to the watershed."
We have revised as suggested.

226-227. Used as a covariate in… (finish the thought).
We have revised to finish the thought.

230-275. This section needs some attention. First, the authors never explain what models are actually being run and compared— this could be in a table, or in the narrative of the text or both. Second, I would provide a citation for AIC (Burnham and Anderson 2002 is the usual one), since those methods aren't given. Third, the writing switches back and forth between past and present tense, which is for the most part unnecessary and distracting. Fourth, some terms are used rather loosely. E.g., "Model fit was based on maximum likelihood estimators…" Do you mean to say models were fit by maximum likelihood? Or do you want to say something about model fit? Also, "within 2 AIC" sounds odd… maybe "within 2 points" or "within 2 units"?
We have revised paragraphs to clarify.

272-275. I would treat elevation as an alternative model, and merge this into the previous section. One sentence paragraphs and sections are best avoided unless you're writing for the BBC.
We have revised as suggested and included elevation as a predictor variable to a single model selection table results.

283-289. I don't agree with this. Certainly it's possible to model bull trout presence as a response to brook trout. If the collinearity with temperature is too high (r=0.56 is borderline, but you could also assess based on VIF), it can be treated as an alternative hypothesis, just like elevation. I'm sure the authors are correct and this won't change the results, but it would be cleaner and less arbitrary to consider this as one of the several hypotheses for explaining bull trout pres/abs.

The inclusion of an evaluation of uninformative parameters as described in Arnold (2010) allows us to keep brook trout in the modeling procedures, but not surprisingly it is an uninformative parameter given the low number of sites where brook trout occurred. It is this low sample size that is likely driving the inability to parameterize this coefficient well. That said we have worked to further evaluate the importance of brook trout through our post-hoc examination of the data. We have no indication that brook trout are expanding in this basin and driving extirpation probabilities, in fact the occurrence of brook trout have decreased over time(one fewer tributary and generally they are in lower abundance than before 2000).

299-302. I don't think this decision is justified; it seems very arbitrary. Season is not really supported as a covariate. Note that because AIC only gives a penalty of 2 for each parameter, adding an uninformative parameter to a good model will produce a model that is always within 2 points of the good one. That doesn't make it a valid alternative. You could add sock color of the field crew as a covariate and get a model within 2 points. This is an underappreciated drawback of AIC, but it has been discussed by Burnham and Anderson and others. I'd start with:
Arnold T (2010) Uninformative parameters and model selection using Akaike's Information Criterion. J Wildl Manage 74:1175–1178.
We agree and have removed season as a covariate in the probability of detection. It does not change the result of our analyses.

308-310. Most of these models are not actually good alternatives, for the reason explained above. In fact, all but five models in Table 2 include "useless" parameters (per Arnold 2010) and I would not include them in the table nor would I include them in model averaged estimates.
Model averaging across uninformative parameters is common approach to dealing with them and even Arnold (2010) highlight one of the five approaches to dealing with them. That said, we completely agree with the reviewer that it is not be the best approach for this study and have considered the approaches highlighted in Arnold (2010). Thus, we have reported models that evaluate our hypotheses but have worked to eliminate non-informative parameters based on their influence on the model (change in AIC in nested models and confidence interval of coefficients, b/SE) from our final models. Then as Arnold (2010) suggests we model averaged the top models containing only informative parameters (no covariates, temperature and elevation). We would like to highlight that whether we model average across all top models (as in previous analyses) or eliminate uninformative parameters – the general inferences from the analyses are the same. Extirpation rates are greater than recolonization rates and even though there are high standard errors around extirpation rates, the associated covariates with extirpation rates are temperature and elevation.

310-312. Is there a reference or reasonable basis for judging "significance" based on being > 1 SD from zero? This would be like using an alpha of 0.32. Seems ad hoc and unnecessary.
We were trying to highlight that these were uninformative parameters. We have reframed following suggestions in Arnold (2010).

330-331. This last sentence is confusing, and may not even be a real sentence.
Revised to clarify

Results in general: I would like to see the model-averaged parameter estimates, with standard errors.
Model averaged extirpation probabilities (with their 95% confidence intervals) are in the figures (model-averaged extirpation estimates versus standardized temperature and elevation) and beta coefficients (with SE) for elevation and temperature in our top models are in the table legend of table 2.

338. I don't think the critical element is that the sites are sampled over a longitudinal gradient, but rather that they are on a temperature gradient and resampled over time. "Sampled over a longitudinal gradient" seems like it's referring to longitude, i.e. the X coordinate.
We have reworded to highlight that we sampled over a "river network that incorporates and temperature gradient".

342-343. There's a lot of repetition in this paragraph. I'd cut the sentence "Extirpation rates positively covaried…"
We have revised as suggested.

For the results and discussion in particular, we went through these comments in detail but based on the larger conceptual suggestions from this reviewer and others, we substantially reworked the discussion to address the larger issues of why others may not have detected trends, etc. So the specific editorial changes may no longer be relevant (given the broader revisions) but have worked be concise and remove repetition throughout.
341. I'd just say "20 years" rather than "15 to 20 years."
344-345. More repetition. I'd cut the first half of the sentence, "Even though extirpation…" and just write, "Extirpation was not related to other habitat variables…"
348-349. I'd cut this sentence too. I'd rewrite the beginning of the next sentence to say, "Our results indicate constriction…"
353-354. I'd cut this first clause and rewrite the sentence to say, "We have no evidence of other changes at low elevation sites (such as development, barriers, or grazing management) that would create inhospitable conditions over the course of the last 20 years."
357-358. I'd cut this sentence, too.
377. Cut the introductory clause. It's already been repeatedly stated that there is a temperature relationship.
377- 382. But burn impacts are in the temperature model (lines 198-202), correct? I think the authors should point this out here, rather than concluding "fire did not predict changes in occupancy," as the burn severity parameter doesn't truly isolate fire effects.
The burn severity parameter does isolate fire effects, especially when it is in the model as a single covariate. The temperature covariate is driven by multiple factors including increases in air temperature, changes in discharge, as well as solar radiation (and canopy cover or shading is influenced by fire). So, we do have some effects of loss of shading from the 2000 fires on the temperature predictions. We have refined the discussion of fire effects in the discussion and tried to clarify this issue.

407. "e.g." not "i.e."
451. Cut the first sentence.
452-457. The connection between the ideas in these two sentences is unclear.
We have revised as suggested and to clarify as still applies to our revised discussion.
I think the last paragraph is a little weak and unfocused. It refers to facilitating bull trout conservation. But how, exactly? How do these results enable "optimal design of conservation strategies?" The paragraph also talks vaguely about using these methods elsewhere, but doesn't really go beyond the obvious. I think the discussion needs to be broadened a bit for a journal like GCB. I'd be interested in the authors' thoughts on why it has taken so long to document climate-associated range contractions/shifts in fish, compared to other taxa. Is this mainly a monitoring failure, or are we possibly facing an extirpation/extinction debt owing to delayed responses, for some reason?

We have substantially revised the discussion compared to the previous version to address these comments.

Thank you for the opportunity to review this paper.

Seth Wenger

Reviewer: 3
Comments to the Author
General Comments:
This type of paper is incredibly useful in understanding how species distribution patterns have changed in response to changing climatic conditions, particularly given the relatively few empirical studies and the number of climate-envelope models that are based on extrapolation. This paper could great be enhanced by addressing the limitations of the analysis. In particular, the authors need to consider analytical approaches for quantifying how the current detection estimation (space vs. time) has influenced estimates. Most importantly, however, is my concern of the effect of the observed results for populations that are likely to have dramatically changed in abundance (regional patterns here) that would result in smaller propagules and less fish/lower densities at lower elevations.
This paper would also benefit greatly by a table/figure describing the changes in temperatures experienced across the time periods for the reader to better understand how actual temperatures have changed over this period; not just regional trends in air temperatures (e.g., Figure 1).

Specific comments:
Line 51: Citation format is not consistent with the rest of the document.
We have revised as suggested and worked to make citations properly formatted for this journal and consistent.

Lines 59-60: The authors may want to note that the shifts from snow to rain in the study area are more likely at lower-elevation sites.
Revised as suggested.

Lines 78-80: The inference of specific temperature changes is not appropriate, as these shifts are unlikely to be ubiquitous to other regions (i.e., the authors should consider removing the specific temperatures and change text here).
We have revised to make the inference more general but our goal here is to highlight that water temperatures have been shown to be increasing in the Rocky Mountains, further supporting why coldwater fish in the Rocky Mountain Region are good candidates for demonstrating… "Increases in summer water temperatures of up to 0.3°C/decade have been documented for Rocky Mountain river basins (Isaak et al. 2012b)." See study area section for more specific information regarding our study.

Lines 107-108: Text here is awkward and not clear. What are the authors referring to here with "how well the common surrogate measure of elevation correlated"? Is elevation a surrogate for climate or distributional patterns?
We have revised to clarify.

Line 112: Comma missing from 1055; inconsistent throughout.
We have revised as suggested and checked our numbers

Line 113: USA here has no periods, previously contained periods (title) Line 115: Pinus was noted in previous text. Change accordingly.
We have revised as suggested.

Line 132: Typo: add 's' after State
We have revised as suggested.

Lines 135-137: The Fraley and Shepard reference is driven from work where bull trout are considered nearly all adfluvial fish. Other references exist for bull trout movement patterns in mixed life-history populations and which are supported by empirical data.
The Fraley and Shepard reference is commonly cited for this type of information, but we have incorporated additional citations to highlight the mixed-migration strategy in the Rocky Mountain Region.

Line 140: Salvelinus was already stated; change accordingly.
We have revised as suggested.

Lines 142-144: The first part of this sentence is redundant with the text on Lines 89-90 in the introduction. Text should be changed accordingly.
We have rewritten to remove any redundancies.

Also, consider peer-review supported literature for complex habitat statement.
We have added peer review literature.

Line 168: Here and elsewhere add a dash after 100 and m; current is inconsistent with line 159.
We have ensured consistency in formatting throughout paper.

Lines 169-171: Some justification is needed as to why 2 fish were selected and why the size limit was set at 250 mm. Bull trout can be sexually mature at sizes much smaller than 250 mm as indicated in the literature and reports.
Our goal was to maintain similar methods to the previous work and ensure that we were not including a single "wandering" migratory fish being captured as indicative as present. We have worked to clarify.

Lines 173-174: The use of habitat data from one site to infer habitat probability of occurrence at larger sites is problematic. Numerous small-stream studies have indicated that site-to site differences in stream habitat are very large—indicating that one site, even within a similar area/stream is not indicative of habitat conditions outside of that site (see Larsen et al. 2001, BioScience; Larsen et al. 2004, Canadian Journal of Fisheries and Aquatic Sciences, etc.). Given large site-to-site differences and the fact that bull trout key in to specific habitat types (see extensive literature), this would likely affect the use of covariates in each of the parameters. .
Our reaches are 100m sites within a 500m site. Even though there is variation at a 100m scale, the scale of drivers of LWD scale forest stands and fire is typically substantially larger than this. There are always some limitations when linking to a previous study (we only have LWD over the first 100m from the Rich et al. 2003 work). We have included the site-specific temporal differences in large woody debris and fire among survey periods by including it as a survey parameter (versus site parameter). We have now highlighted in the discussion, why certain parameters we know are important for occupancy may still be

key to occupancy, but not show up as important for *changes* in occupancy or extirpation rates across the landscape.

Lines 178-179: Consider adding the accuracy of the Taudem elevation predictions as this is a key attribute in the analyses and temperature models.
We have highlighted the use of DEM in Taudem, but limited discussion on this to be concise. Taudem uses a DEM to derive hydrologic information (i.e. elevation, channel slope, etc. subsequently used in FireBGC). So, the accuracy of the Taudem predictions reflects the accuracy of its source DEM which was from the National Elevation Dataset (NED) at a 30-m resolution. The vertical accuracy of NED data was tested by comparing it to an independent reference source of very high accuracy and estimated to have RMSE of 2.44 meters (Gesch 2007).
Gesch, D.B., 2007, Chapter 4 – The National Elevation Dataset, in Maune, D., ed., Digital Elevation Model Technologies and Applications: The DEM Users Manual, 2nd Edition: Bethesda, Maryland, American Society for Photogrammetry and Remote Sensing, p. 99-118.

Lines 181-183: With specific boundaries, why did the authors use categories of the presence/absence of fires? Given that understanding the effects of fire was a specific objective, lumping 1% of riparian area burned with 100% burned seems like detecting an effect would be problematic.
There is a strong correlation between % of the riparian zone burned and fire severity. If there is a severe riparian burn, a large percentage of the neighboring area burned. This is now mentioned in the manuscript.

Lines 197-198: Do the authors have an understanding of how well this model, that is calibrated from post-fires, estimates temperatures of streams pre-fires? Particularly given the inputs in the model as described subsequently. If not, the authors should discuss as a limitation and/or consider a sensitivity effort to identify how these errors may influence results.
The residuals are representing the relative difference in temperature among sites on the landscape. We are not highlighting whether bull trout been lost in sites that have warmed the most, but are the warmest on the landscape over the last decade.

Lines 221-227: It would be helpful if the authors described the climate, disturbance (i.e., fire), and biological reasoning for this approach. Overall this approach is interesting, but isn't it essentially inflating the climate effect here? Particularly in describing the effect size of parameters.
Also, wouldn't the most appropriate measure be to sum the residuals from 1996 through 2008 as measures of how the sites changed? I.e., the complete period in between the sampling events?
We calibrated FireBGCv2 to landscape conditions for the post-2000 period by using Landsat satellite imagery from 2004 and interpreting to describe vegetation composition and serial stage across the entire landscape – both in burned and unburned areas. We did compare FireBGCv2 temperature predictions to field observations. We validated the regression equation by comparing observations from 24 digital thermographs monitored from August 2010 to August 2011, to stream temperatures predicted by implementing the daily maximum equation in FireBGCv2 for this same period. FireBGCv2 modeling compared reasonably well to observed values (r_s = 0.83, MAE = 2.59°C, RMSE = 3.42°C) but suggested a tendency for FireBGCv2 to over-predict stream temperature. The validation dataset however may also be skewed towards warmer temperatures since thermographs were distributed across only a subset of the EFBR subwatersheds with a considerable concentration in warmer reaches. Again, the question is – are we seeing extirpation probabilities in the warmest sites on the landscape over the last decade? (not change in temperature over the last 20 years). We highlight the link between our water temperature predictions and fire in the discussion more extensively now.

Lines 253-254: What assumptions are there when pooling across years in this type of Robust Design approach?

There are assumptions in pooling across years, using 2 years of sampling as a snapshot. But given the life history (mostly resident fish and relatively long life-span), this isn't a fast changing species. In addition, we did use space for time in the probability of detection function (which is a different issue) but minimized several concerns of pooling between years within any probability of detection function.

Lines 260-261: Extirpation is more commonly referred to as "Epsilon" after the Greek letter..

Revised as suggested

Lines 267-269: This sentence or portions are redundant with text on lines 248-250.

Revised to clarify

Lines 269-270: Consider model averaging across all models; the benefits from a multi-model approach is to incorporate the parameter estimates from all competing models. Models between 2 and 4 delta AIC in particular can influence parameter estimates and our understanding of the uncertainty surrounding these estimates. This is particularly true given the results in Table 2 where there really is no clear top model: top model weight is 8.8%.

Based on comments from reviewer 2, instead of model averaging across more models with uninformative or useless parameters we have refined our reporting to those results that highlight key results as suggested in Arnold 2010.

Lines 285-286: Describe significance level in methods and/or remove term 'significantly'.

We were trying to highlight the low betas (effect sizes) and their high uncertainty. This was just a piece of evidence to highlight that these were uninformative variables. We have reframed using Arnold 2010.

Lines 292-294: Consider moving to the methods section.

We have revised as suggested.

Lines 292-302: The authors should provide information on the real detection estimates with SE for an understanding why there is such variability in subsequent estimates.

We have added a reporting of the average and range of our site specific probability of detection estimates in comparison with other studies in the results.

Lines 299-301: Given that AIC resulted in the top model that was 1.75 delta AIC from the next model, and the authors decision to use an AIC framework, it is surprising that the authors would "choose" the model for the analysis. The authors should describe the similarities/differences in real estimates across seasons and models for the reader.

We have reanalyzed the data without season as a covariate in the probability of detection function.

Lines 305-307: While the authors do find considerable differences in extirpation and colonization, there is large confidence intervals around these estimates. With considerable overlap in CIs of real estimates and I presume betas, the inference becomes weaker.

True and this is highlighted in the text.

Lines 316-320: See comment above for use of fire data.

Lines 323-332: Where is the table associated with the elevation comparison? Were there any other covariates used in the model assessments of extirpation and colonization? The authors should consider providing a straight comparison of probability of extirpation and colonization on a figure with elevation on the x-axis and temperature on the y-axis. The current results really don't test the objective here which was: "How well the common surrogate…." (See lines 107-108).

We have revised to clarify. In general, many predictions models use elevation as an individual measure of how bull trout populations will change (with the prediction that they will be reduced to high elevation thermal refuges if flooding or exotics do not keep them from surviving in these places.) So, we wanted to examine whether elevation was associated with extirpation probabilities. Our plots of model averaged extirpation versus the standardized temperature and elevation is in the manuscript, but have tried to clarify the questions regarding elevation and have increased information in discussion section as well.

Lines 348-349: The use of "influence" is not appropriate here.

We have revised the sentence.

Lines 387-392: Use of Oncorhynchus should be on Line 387, not here, where it should be abbreviated.

It is in the methods so should be abbreviated in both places here.

Line 398: Typo on "became".

Fixed

Lines 411-412: Use of terminology "..solid methodologies.." is not appropriate and not clear.

Revised

Lines 415-419: This section is redundant with study limitations section and in methods. Further, despite the references, the assumptions that are stated by MacKenzie and others is if this approach (using space vs. time) is appropriate biologically. Bull trout are known to be clumped in distribution and are strongly associated with habitat characteristics.

We discuss the potential bias associated with using 100-m reaches for probability of detection and explored whether it is likely biasing our estimates but 100-m reaches within a 500-m site has not changed between surveys and bull trout can readily move this short distance.

Lines 422-423: Given that habitat complexity can change dramatically across individual years, it is unlikely that the potential bias would be similar across time periods. We have no understanding if the factors that influence detection equally across time periods.

True, most of our variables specifically gradient, width, elevation did not change substantially across time within our reaches, but large woody debris did especially with fire so we have used large woody debris as a survey covariate (changing for each survey based on the large woody debris data at time of fish survey) not a site covariate.

Lines 429-432: This section is unnecessary.

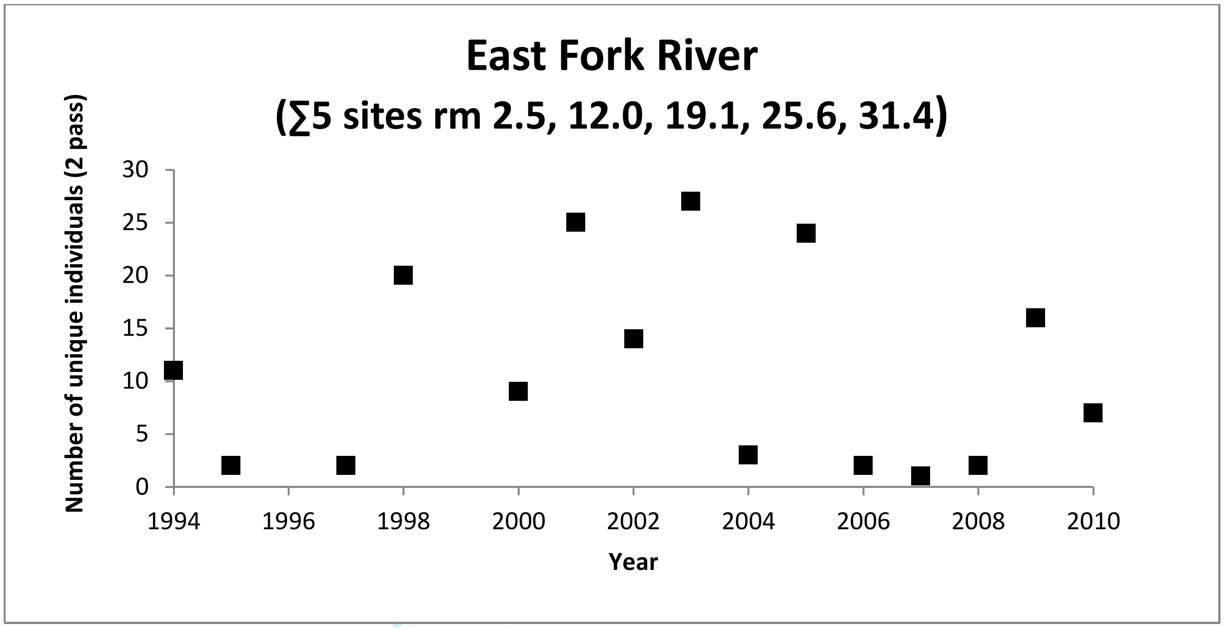
We have removed

Lines 433-450: This is the greatest limitation to this study. Bull trout can display large fluctuations and have demonstrated large fluctuations over the period included in this study. Regionally, bull trout have displayed considerable declines in abundance from the early nineties until this recently, even in populations where temperatures are not ~limiting. It is surprising that the authors did not use 1-pass

electrofishing as a surrogate for relative density in their analyses. This may help account for the large variability in extinction and colonization. Bull trout populations can have very low densities, particularly at lower-elevation locations. This pattern can be even more pronounced when overall abundance is lower. This pattern is likely have large effects on this type of analysis, and renders the need to consider population abundance. If abundance is not possible, perhaps some measure of distance to large river, which was stated earlier as a key attribute for bull trout, may be interesting to include.
AND
Lines 443-446: This is confusing. In Montana bull trout have shown to experience large fluctuations. In this section are the authors saying bull trout abundance is associated with stream flow? (see line 444). Has this 3 to 4 year time lag been demonstrated? The reference to peak and valley is occurring over this time period for many populations, making detrending this pattern necessary for this type of analysis. Generally salmonids have been shown to fluctuation in some systems and for these types of studies it is key to address as a discussion topic. In Myers and Copeland, there were small fluctuations in bull trout populations, but primarily bull trout are declining. We have not found any published data that bull trout in MT are cycling. In Rieman and McIntyre redd counts in streams nearby are more highly correlated than distant populations, but are still only weakly correlated and the larger effect was that populations in three of the four watersheds were declining (but declined during the 1980s and early 1990s—before this study).

The initial protocol was developed for presence/absence data assessment, not relative abundance estimates. That said, we think that the extirpation rates that we found indicate that the population is declining and constricting its range (so yes, it is likely that the population is declining and we have documented a small amount of range constriction in warmer, lower elevation sites as most climate change models are predicting). In our search for data for bull trout in western Montana, most of the population declines were before 92-95 (this drove much of the impetus for listing) but many of these declines has leveled off since the early 90s. The only exception that we found is the Swan River drainage where bull trout redd counts declined more recently after lake trout were found in the basin.

Bull trout are declining in different areas throughout their range due to exotic species in rivers and lakes, human impacts, as well as habitat degradation. As discussed in the manuscript, we are not in an area with lake trout, brook trout have not expanded in this area, and currently brown trout are rare in the tributaries sampled. There have not been substantial shifts in human disturbance in the watersheds, but in this area over the time period of the study there has been wildfire and general stream/river temperature warming. In addition, looking at unpublished MFWP data, tributaries are on their own, different trajectories but if we examine bull trout captured in the East Fork River (number of unique individuals but averaging across river sites) in the Bitterroot data set (see figure below).



Since relative abundance in main-stem river environments has been shown to predict occupancy (Rich et al. 2002), we have included rank distance to where bull trout are common in the analyses.

Lines 451-452: This is a weak topic sentence and should be revised.
and
Lines 451-465: This entire section is uncecessary.
We have revised to improve the end of the manuscript